

The Biology of *Colias blameyi*(Pieridae), the "Green Sulphur" of the Argentine Puna

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Abstract. *Colias blameyi* Joergensen is a high-altitude endemic found in the puna of the Provinces of Catamarca, Tucumán, Salta and Jujuy in northwestern Argentina. It is probably double-brooded, with a seasonal up-and-downslope migration tracking the availability of its host plants, *Astragalus* spp. (Leguminosae). The early stages, reared on alfalfa (*Medicago sativa* L.) are described. The relationship of *C. blameyi* to other taxa of high-altitude Sulphurs in the central Andes remains problematical.

Introduction

The biogeography of the high-Andean butterfly fauna is receiving renewed attention in the context of attempts to reconstruct Quaternary climate dynamics and their impact on biotic diversity in tropical America (Brown 1987, Descimon 1986, Shapiro 1989). For most groups, both distributional and biological data are still inadequate for a proper analysis to be done. In many cases the sister-groups of endemic Andean taxa are unknown. The genus *Colias* has its greatest diversity in the Holarctic, but has undergone considerable adaptive radiation in the cold and temperate parts of South America. The systematic position of the Andean *Colias* is far from resolved. Descimon (1986) considers them a monophyletic group, while Berger (1986), in a global revision at the subgeneric level, does not. The characters used by Berger to delimit subgenera are superficial and poorly if at all rationalized, while Descimon's discussion is informal and his bases for judgment are inexplicit. Speculation must be replaced by data if progress is to occur. Descimon has reared several Andean *Colias* and indicates (*loc. cit.*) that their life-histories will be published. One which he has not reared is *Colias blameyi* Joergensen, whose life-history is reported here.

In 1916 Pedro Joergensen, one of the three founders of Argentine Lepidopterology (with Eugenio Giacomelli and Carlos Berg), published a landmark monograph on the Argentine Pieridae which included the description of a new *Colias* from the Sierra de Aconquija, Provinces of Catamarca and Tucumán. The Sierra de Aconquija and Cumbres Calchaquíes form a major eastern outlier of the Andes proper, reaching altitudes over 5000 m (Nevado del Candado, near the southern end of the Aconquija range, reaches 5450 m), and separated from the Andes by a deep trough, the Valles Calchaquíes. Moisture-bearing winds strike

the range from the east, so that there is a very pronounced rain shadow west of the crest. The seasonally wet climates east of the crest provide the last refuge for many humid-Neotropical biotic elements of the mid-elevation forest zone, while the subalpine and alpine zones shelter many elements of the central Andes (Peru, Bolivia) which drop out in the Andes themselves south of the Province of Salta. Joergensen was able to mount several expeditions into the Aconquija range with the help of his friend Joel Blamey of Huazán, after whom he named his new Sulphur. There was a burst of description of new Andean *Colias* around this time, but as usual they were published in European journals and Joergensen was unaware of them; for him the dusky green phenotype of *Colias blameyi* was something entirely new for the continent, and it immediately reminded him of various boreal Holarctic species: "The male of this new little species... cannot be confused with any of its South American congeners, but it has the size and the dark glaucous green ground color of the species *nastes* Boisduval and *behri* Edwards, the former from the North American Arctic (Labrador, Greenland, Alaska and British Columbia), the latter from the mountains of California; but the patterns are different." (Translation by A.M.S.) He provided an excellent, detailed description of both sexes and a brief summary of what he knew of its biology. Since then this striking insect has been collected occasionally by travelers, but nothing further on its biology has appeared. If Kenneth Hayward knew any more about it, his information apparently died with him, as the projected Pierid volume in Hayward's monograph of the Argentine butterflies never appeared and no manuscript has been found. Although several South American *Colias* have been reared, the only species for which published information on the life-history and early stages is available is *C. lesbia* Fabricius, which is a serious alfalfa pest in several countries. It has been monographed by Biezanko (1954), Freiberg (1947), and Reed (1922). Although *C. blameyi* is common in the proper habitat in season, specimens are rare in collections — even in Argentina itself.

Biology of Adults

Joergensen (1916, p.510) states that *C. blameyi* "is common on the summits of the grassy mountains: Cerro La Tambilla, 3700 m; Cerro Medio, 3750 m; Cerro Yutoyaco, 3500; Cerro Negro, 3500, and Cerro La Ensenada, 3200. All these localities are east and southeast of the snowy summits of the Aconquija range. There it flies from the end of January until the end of April. Its flight is not very high, but in good weather it seems constantly in motion, (though) often settling on the ground or on flowers such as *Gutierrezia repens* Gr., *Hypochaeris meyeniana* Wolp. (Compositae), *Verbena microphylla* H.B.K. (Verbenaceae), *Malvastrum capitatum* Gr, and *M. parnassifolium* Hook. (Malvaceae). When the hard freezes begin on the heights in late March, it descends... to more protected valleys, for example at La Ollada (3100 m), where it is never

found in summer." Joergensen was an excellent observer and is correct on all points.

There is no amplification of the range, as stated by Joergensen, in any subsequent literature. Because the closely related entity *C. weberbaueri* Strand, which differs from *c. blameyi* primarily in its lack of an androconial patch in the male, is the only taxon of the group recorded in Bolivia, it is important to note that *C. blameyi* is not confined to the Sierra de Aconquija. Within the Province of Tucumán it extends north an indeterminate distance well into the Cumbres Calchaquíes, which extend to the NE of Abra Infernillo (3300 m), where Highway 307 (Monteros-Amaichá del Valle) crosses the range. In the true Andean *puna* it, or an entity transitional from it to *C. weberbaueri*, occurs abundantly in the Provinces of Jujuy (Abra Pampa, Tres Cruces, Esquinas Blancas, 3693-3875 m, all along Highway 9 above Humahuaca) and Salta (Cuesta del Obispo, Abra Molina, Cerro Zapallar, Valle Encantado, all along or near Highway 33). There is great individual and interpopulational variability in both sexes (figs. 1,2). *Puna* animals average lighter than Tucumán and Catamarca ones, but nearly all have well-developed androconial patches. There is no obvious tendency for them to be smaller, or more frequently reduced, in the *puna* than in the Aconquija-Cumbres Calchaquíes populations.

Both sexes fly from roughly 1000 to 1500 daily in good weather. Flight initiation in the morning occurs with air temperatures of roughly 10°C with light wind and strong sunshine. Flight may be terminated early by cloudiness or, even under clear sky, by strong and turbulent upslope afternoon winds which often develop on the eastern slopes of the Tucumán-Catamarca ranges and at the head of the Quebrada de Humahuaca. A few animals continue to fly in the lee of ridges or hills until the sun fails to reach them.

Males patrol linear habitats such as roadsides, streamsides and gullies, and below the crests of ridges, but do not hilltop. They can often be seen coursing back and forth over alpine grassland and rock gardens (as in fig.3) about 1 m above the ground. All-male aggregations occur on moist earth, at puddles and along streambanks. Up to 30 animals have been seen puddling together, mainly after 1330. Females occur singly and are seldom seen where males are patrolling. Most of my observations of females have been at or near summits, where host plants grow among rocks, or around shrubs, where they often grow within the drip line. Oviposition occurs singly, usually on the underside of a leaf, and females will frequently proceed in more or less of a straight line, laying one egg on each plant they encounter.

Host Plants

Three definite hosts have been identified (by R. Barneby, New York Botanic Garden). All are based on many (> 10) oviposition records/each.

They are *Astragalus garbancillo* Cav. and *A. micranthellus* Wedd., both at Tres Cruces, Jujuy, 3800 m \pm , and *A. hypsogenus* I.M. Johnston, at both the summit of Cerro Zapallar, ca. 4200 m, Salta, and on several summits near Abra Infiernillo, Tucumán, ca. 3500 m (all Leguminosae).

These three species are disparate in both facies and phylogenetic affinities. Their differences imply that *C. blameyi* is a generalist at least within the genus *Astragalus*. *Astragalus* is very well-developed and diverse in the Andes (Johnston 1947). *A. garbancillo* is "the most widely distributed and most commonly collected South American *Astragalus*" (Johnston 1947, p. 384). It is erect and ascending in habit. In Argentina it is largely confined to moist and dissected areas at the periphery of the puna. It is a common species in much of the range of *C. weberbaueri* in Bolivia and Peru and should be considered a probable host. It is taxonomically isolated within the genus *Astragalus*.

Astragalus micranthellus is depressed, prostrate to tufted and much less leafy and conspicuous than *A. garbancillo*. Its range includes *altiplano* and *puna* in Peru and Bolivia, extending in Argentina only as far south as the Sierra de Aconquija (Johnston, p. 391).

Astragalus hypsogenus is a small, tufted plant with tiny leaves but very showy purple flowers, reminiscent in habit of some of the alpine *Lupinus*. It is one of the aspect dominants of alpine rock garden habitats on the wetter summits in both Salta and the Aconquija-Cumbres Calchaquíes and grows in the sites shown in both figs. 3 and 4. Its range includes Bolivia and northern Argentina, again not south of the Sierra de Aconquija. It forms a compact, isolated species-group along with *A. confinis* I.M. Johnston and *A. crymophilus* I.M. Johnston.

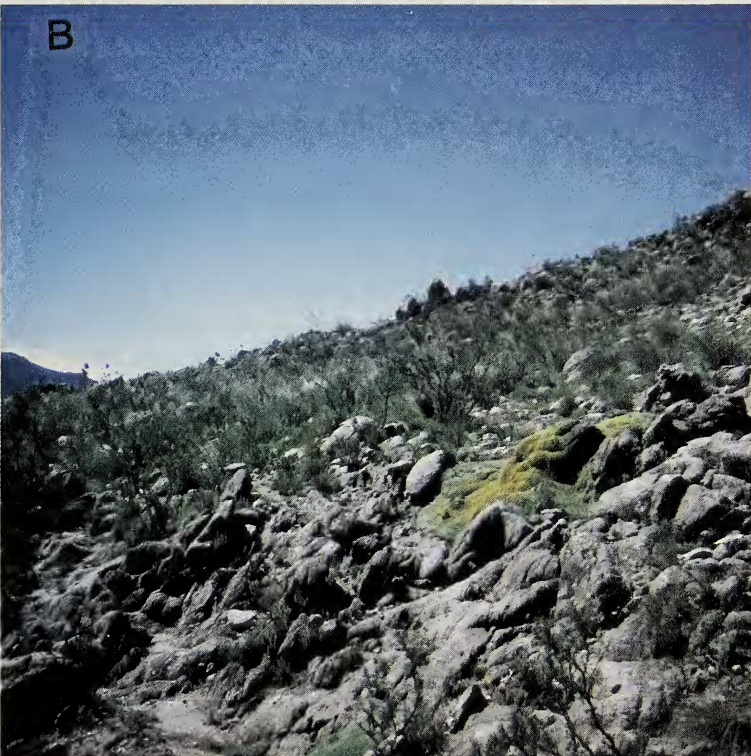
Both *A. garbancillo* and *A. micranthellus* are confirmed wild hosts of the pierine *Tatochila distincta distincta* Joergensen, which can however be reared on Crucifers in the laboratory (Shapiro 1986). This butterfly co-occurs with *A. hypsogenus* in both Salta and Tucumán, as does the very rare and as yet unreared *T. inversa* Hayward.

Early Stages

No significant differences have been observed in material from Salta, Jujuy and Tucumán. Rearing was done at Davis on alfalfa (*Medicago*

Fig. 1. *Colias blameyi* from these disjunct populations in northwestern Argentina, males at left. A: Quebrada Carapunco, Province of Tucumán, 20.i.1986. B: Esquinas Blancas, Province of Jujuy, 7.ii.1984. C: Summit of Cerro Zapallar, Province of Salta, 22.i.1986. The Tucumán populations are essentially topotypical. The Salta and Jujuy populations resemble *C. weberbaueri* from Bolivia but have well-developed androconial patches in the males.





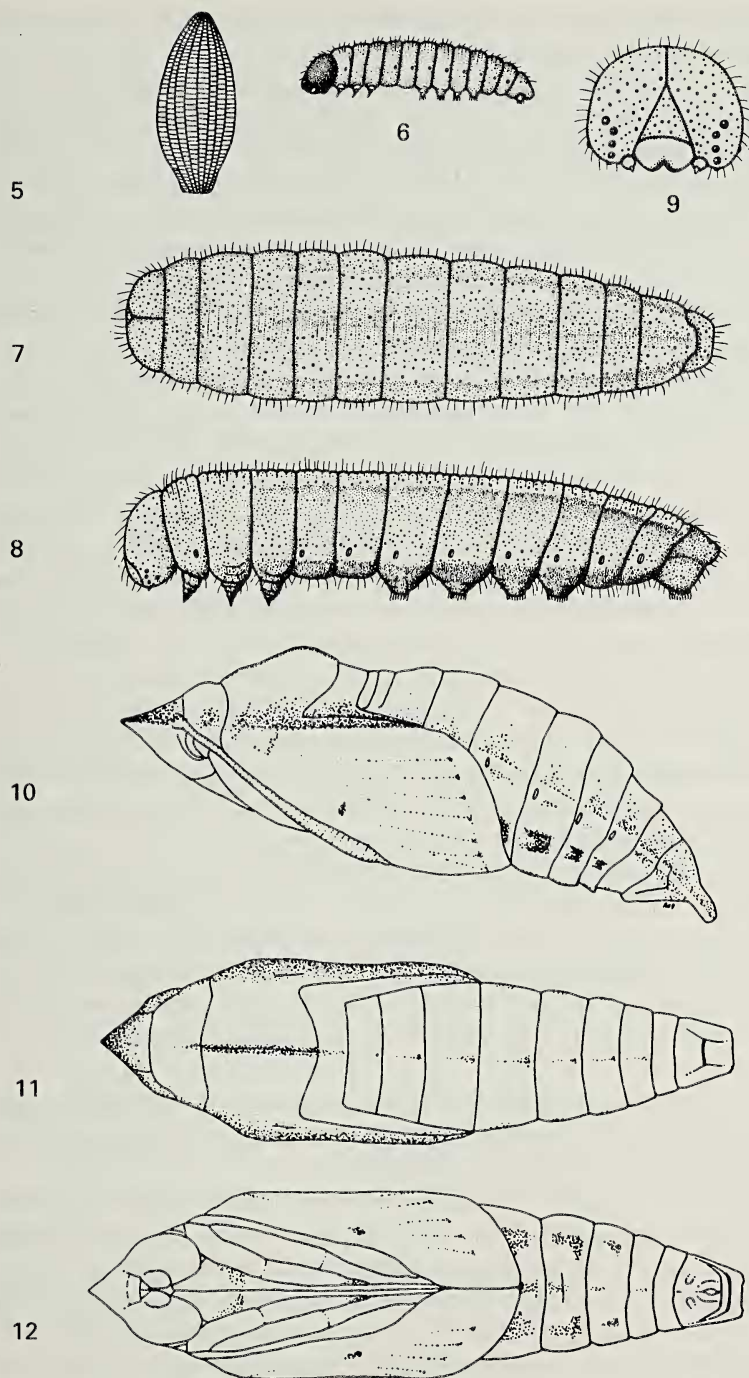
sativa L.) cuttings; *Vicia benghalensis* L. was eaten but no larvae survived beyond the third instar on it. Larvae were kept in plastic Petri dishes under 14L:10D, 23.9°/12.8°C. Preserved early stages have been retained at Davis. All color descriptions are from life. Those in parentheses refer to the color-standards system of Kornerup and Wanscher (1978).

Egg (fig. 5). — Erect, fusiform, strongly tapered at both ends, 1.1×0.3 mm, the chorion sculptured as figured with about 16-17 and 42-52 vertical and horizontal ribs. Madder red (9A7) when laid, becoming translucent about 12 hr before hatching. Laid singly, usually on lower leaf surfaces. Newly-hatched larvae do not eat their eggshells. Time to hatch, 7-8 days.

Larva: First Instar (fig. 6). — At hatch 1.15 mm, grayish to brownish orange, the head much darker; head and body with pale, mostly glandular hairs disposed as below. After feeding grayish green (1D7) dorsally, grayish yellow (1B3) ventrally, a darker shade immediately below the spiracles and above the prolegs, gradually lightening toward the venter. First thoracic segment with a transverse fold and 9-10 glandular hairs in a single row. Second and third segments with folds dividing them into five annulae, the fourth (counting caudad) bearing 8 glandular hairs in a single transverse row. First two abdominal segments each with four annulae, of which the first and fourth each bear two glandular hairs. Other abdominal segments with five annulae, the first and fifth of which each bear two glandular hairs, except the eighth and ninth with three annulae, two hairs each on first and third; and the last with a darkened sclerotized shield bearing several dark, non-glandular setae, plus six glandular hairs anterior to the shield. Excavates strips of parenchyma; feeds by day and night and rests along the midrib. Length of instar, 3-4 days.

Second Instar. — After molt 3.8 mm. Similar, with annulae disposed as follows: five annulae per segment except the following abdominal segments with six: second, fourth, fifth, seventh; third with seven; ninth and tenth apparently unitary. This arrangement is continued in later instars, with intercalation of annulae on some segments especially near the front of the abdomen. Dorsal and lateral surfaces densely covered with small dark tubercles in two sizes, each surmounted by either a

Fig. 2. Habitats of *C. blameyi* in wet season, during the flight period. A: Summit of Cerro Zapallar, Salta, looking toward Valle Encantado below. Both sexes are common here, flying over alpine rock gardens. B: Rocky summit at about 3900 m in the Cumbres Calchaquíes near Abra Infiernillo, Tucumán. Females occur here and oviposit on *Astragalus hypsogenus* among the rocks. The yellowish cushion plant is *Azorella* (Umbelliferae, "yareta"), a characteristic alpine plant in the region.



Figs. 5-12. Life history of *C. blameyi*. 5, egg; 6, first-instar larva, lateral view; 7, fifth-instar larva, dorsal view; 8, same, lateral view; 9, same, head capsule; 10, pupa, lateral view; 11, same, dorsal; 12, same, ventral.

glandular or a simple hair. Head darker than body, densely tuberculate. No change in habits. Duration, 3-4 days.

Third Instar. — After molt 5.25 mm. Similar, tubercles densely and rather evenly distributed over dorsal and lateral surfaces of body and even more densely on head, the larger ones darker and bearing mostly dark hairs, the smaller either darker or concolorous and bearing either dark or pale hairs. Head capsule scarcely darker than body: ocelli black. A vague pale line on each side incorporating the spiracles; directly below it a very dark shade of the ground color, grading insensibly into the paler venter. Third instars consume epidermis as well as parenchyma. Length of instar, 4-5 days.

Fourth Instar. — After molt 8.5 mm. Similar, with a decidedly granular appearance due to the very numerous tubercles and hairs. Rests lengthwise on the petiole when not feeding. Length of instar, 5 days.

Fifth Instar (figs. 7, 8, 9). — After molt 14 mm, reaching 23 mm at maturity. Head and body above olive (2E6) with numerous tubercles, both dark and concolorous, over the dorsal and lateral surfaces; hairs both light and dark, between 50-100 per annulus. Spiracles not contrasting, but incorporated in an ill-defined pale line (grayish yellow, 1B3) not enclosing any red or pink color; below this a darker shade of the ground color, passing into dull olive (2D4) just above the bases of the legs, which are concolorous with the venter. Crochets black. Dorsal midline slightly darker than ground; the entire dorsum slightly paler than the sides, the pale hue ending abruptly where the subdorsal pale stripes would be if present. Head dark olive, densely tuberculate, the tubercles bearing dark hairs; ocelli brownish-black.

The mature larva feeds by day and night in the lab, resting on stems. If disturbed, it drops to the ground in a coil, reascending the plant 10-15 min later. This is a stereotyped defensive reaction in all *Colias* I have reared. The day before pupation the larva turns grayish with a slightly purple tinge, leaves the plant and wanders for several hours before spinning a mat of silk in preparation for the molt. Duration of instar, 7-10 days.

Prepupa. — Formed vertically, head up, pendant by the silken girdle and attached at the cremaster, appearing greasy and grayish-yellow-green. Length of prepupal period 20-36 hr.

Pupa (figs. 10, 11, 12). — Typical *Colias* form, chunky, the wing-cases not particularly inflated and the frontal prominence short and broad; length 14-15 mm, width at base of abdomen 3.3-4 mm. Dorsal surface olive yellow (2C7); ventral, including wing cases, canary yellow (2B7). Proboscis not reaching tips of wing cases. Wings with a black dot corresponding to the discocellular spot of the adult and black dots at the vein-tips. Brownish-red (10C7) shading as follows: on dorsal surface of the frontal prominence; along hind margin of wing cases; on the dorsal thoracic keel; above the spiracles; and two parallel rows of blotches on the ventral abdomen, one on either side of the midline. Spiracles

enclosed in a yellowish-white, moderately contrasting line. Eyes, wings and body becoming pigmented in that order the day before eclosion, the wings of both sexes initially yellowish-white, those of the males subsequently turning dark (black pigment laid down several hr after white). First meconium dull rose pink, second colorless. Time to hatch, 12-17 days.

Diapause. — *Colias* usually diapause as third-instar larvae. Several larvae indeed stopped feeding in the third instar and survived 2-4 wk thereafter, but there was so much disease mortality that I cannot say with confidence that they were attempting to diapause. Altitudinal migration, such as between La Ollada and the Sierra de Aconquija or between Valle Encantado and the summit of Cerro Zapallar, may be a seasonal strategy to avoid severe cold and to track host plant availability. In many insects such migration substitutes for diapause as a mechanism to avoid seasonal stress. *Colias blameyi*, however, disappears altogether for more than half the year and diapause is thus very likely. Descimon (1986) echoes other authorities in recording the entire assemblage of pale and green *puna* species as flying only in rainy season ("March-April, or December in the Arequipa region").

Altitudinal migration appears to be very common in the butterfly fauna of the northwestern Argentine highlands. Several species of *Tatochila*, including *T. sterodice macrodice* Stgr., *T. stigmadice* Stgr. and *T. orthodice* Weymer, which fly with *C. blameyi* in January and February, can be found at much lower elevations in the Provinces of Salta and Tucumán in November. The member of the *Phulia nymphula* Blanchard complex (*aconquijae* Joerg.) found in the Aconquija and Cumbres Calchaquíes parallels *C. blameyi* in its winter retreat to the level of La Ollada.

Comparisons to C. lesbia. — *Colias lesbia* is larger (except in cold-weather broods) throughout its development, and both the larva and pupa are more slender. The disposition of annulae and glandular hairs on the first-instar larva is very similar, but the number of annulae diverges in later instars. The larva of *C. lesbia* is bright "alfalfa green" rather than dull or olivaceous green as in *C. blameyi*, and has a pink spiracular line. The pupa is brighter green and has a bolder spiracular line with silvery reflections. Both morphology and pattern are very conservative in *Colias* immatures, as noted by Descimon (1986). Until a detailed morphological study is done of representative members of various species-groups, isolated rearings will cast little light on the Holarctic sister-group of the Andean group to which *C. blameyi* belongs; the relevant information is still largely lacking for the Holarctic taxa as well. There is nothing in these descriptions which would lead one to question the joint membership of *C. lesbia* and *C. blameyi* in a monophyletic Andean group, but the point is moot until more descriptions are available. All of the Andean species reared so far are Legume feeders, though some are presently known only from naturalized European clovers.

Discussion

The group of taxa embracing *C. blameyi*, *C. weberbaueri*, *C. erika* Lamas, and *C. mossi* Rothschild (including "form" *nigerrima* Fassl), all from Peru; and *C. flaveola* from Chile (and northwestern Argentina, Shapiro, unpublished), is badly in need of revision. Of the heavily melanized taxa only *weberbaueri* is recorded in Bolivia, but *blameyi* is now recorded within about 25 km of the Argentine-Bolivian border in the *puna* of Jujuy, and *flaveola* is now known to cross the Andean crest and penetrate the eastern slope. Berger (1986) treats *blameyi* as a subspecies of *mossi* but *weberbaueri* becomes a separate species by virtue of its lack of an androconial patch. Descimon (1986, p. 506) states that this is a fluctuating character in some populations, even of *flaveola*. Shapiro (1985) has published a figure of a melanic aberration of *C. euxanthe stuebeli* Reiss. from the Department of Cusco, Peru. The type of melanization displayed is quite different from that of melanic aberration of the Nearctic *C. philodice* Godt. and *C. eurytheme* Bdv. but agrees perfectly with that seen in the *puna* complex, underscoring the point that phenotypic similarity within this group could easily have arisen by parallelism. It cannot be assumed automatically that all the "green" taxa are more closely related among themselves than they are to the non-"green" ones.

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